THE DEVELOPMENT OF THE HAIRS UPON THE WINGS OF PLATYPHYLAX DESIGNATUS WALK.

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While it has been assumed that the hairs on the wings of the Trichoptera develop in exactly the same way as those upon the wings of the Lepidoptera there is, so far as we know, no definite work to show that this assumption is correct. The following study was therefore undertaken to definitely ascertain, in some one species of Trichoptera, in what manner these hairs did develop upon the surface of the wings and *Platyphylax designatus* was selected for the work.

It has been impossible to find any works which could be given as an historical review of the subject and those papers having to do with the development of the wing of the caddis-flies have been given in a former paper (5). Dewitz (3), from whose work comes most of our previous knowledge of the development of the wings in this group of insects, does not take up the formation of the wing hairs. Spuler (9) distinguishes between hair scales and those hairs without a circular ring-like base for articulation and he shows a surface view of a portion of the wing of a Trichopteran, *Philopotamus scopulorum*, with a few of the latter hairs and four of the ring-like bases into which the hair scales are inserted. Regarding these structures he says: "Die gleichen Gebilde (hairs) finden wir auch bei den Trichopteren, gerade die Micropteryginen und Hepialiden, in der Flügelbidlung so nahe den allgemeinen Modus der Haarbildung vor sich. Dieselben werden von der Hypodermis gebildet. Jeder Stachel ist seiner Bildung nach unicellular." Tower (11) reaches a similar conclusion, saying: "In development the scales of Coleoptera follow exactly the same course as was found by Mayer (6) in the Lepidoptera."

The wings of *Platyphylax designatus* are more or less covered with hairs; these are present upon all the wings and on both surfaces although the anterior wings show a greater degree of pubescence than the posterior and the upper surface bears a much larger number of hairs than the lower. These hairs can be roughly divided into four groups: 1, vein and marginal hairs; 2, large surface hairs; 3, small surface hairs; 4, special long hairs.

1, vein and marginal hairs. The vein hairs are in most cases in a single row on nearly all of the longitudinal veins and are apt to be equidistant from each other; this is not true for the entire course of each vein as the hairs generally come closer and closer together in passing from the distal to the proximal part of the vein. Besides what one might call the ordinary vein hairs there are a number of very much smaller ones which, upon many of the veins, alternate with the larger hairs; on account of the prominence of the regular vein hairs these smaller ones are not at first likely to be seen. The vein hairs are mostly restricted to the upper surface and are more numerous and larger on the anterior than upon the posterior wings. The longest and thickest vein hairs are found near the base of the anterior wing, these are fluted, with many small ridges running lengthwise along the hair giving it the appearance of a cog wheel in transverse section (Fig. 1).

The marginal hairs, similar in size and structure to the vein hairs, are found not only upon the extreme margin of the wing but they extend for a short distance on to both the upper and the lower surfaces. In the anterior wing these hairs are longest, all lie close down against the margin and are directed toward the apex of the wing. Along the anterior margin of the posterior wing these hairs are similar in position to those upon the anterior wing but along its posterior and outer margins they are arranged perpendicular to it; these hairs as well as some upon the surface are plumose, the plumules are very small and not visible until the hairs are examined with a high power of the microscope.

All vein and marginal hairs are widest at the base and gradually taper to a point; they are hollow, nearly all are slightly curved and each fits into a raised ring-like cuticular opening on the surface of the wing.

2. Large surface hairs. Nearly all of these hairs are smaller than those just described, they are also heavier and darker and a little more curved. On the anterior wing these hairs are more numerous than on the posterior one and in both wings they are much more abundant upon the upper surface. On the posterior wing most of these hairs are on its outer third, except a narrow strip running along near the costal margin, and there are several large hairless areas, these are probably due to

the folding of the wing. The circular raised ring into which the hairs fit is smaller and less noticeable than the similar part for vein and marginal hairs. These surface hairs have a pointed distal end, with this exception their diameter changes but little and they do not become widened at the base.

3. Small surface hairs. These are very numerous and are scattered regularly on the surface, vein and margin. They are all nearly equal in size and are bent or hooked near the tip. A surface view of any part of either wing shows that these hairs come from nearly all of the hypodermal cells which have not taken part in the formation of one of the larger hairs.

4. The longest hairs are near the base of the posterior wings, they are much longer than the others and are present upon the surface and on the veins. These long narrow hairs are of equal diameter throughout except the pointed distal end. The ring-like cuticular thickening into which each hair fits is not directly upon the surface but situated upon a rounded papilla. In transverse section these hairs are seen to be fluted, much more deeply so than the large ridged vein hairs; the number of raised ridges varies from five to eight although six is by far the most constant number (Fig. 2).

When the pupa of *Platyphylax designatus* emerges from the last larval skin the wings are found at the sides of the thorax extending down against the legs and by these held from further extension in a ventral direction. In a surface view the wings are seen to have several longitudinal folds, Marshall (Fig. 23), and in section to have a fluted appearance along both surfaces. The wings soon begin to unfold and straighten until they are extended backward along the sides of the abdomen, Marshall (Fig. 25). The thickness of the wing does not at first decrease and in section the cells of the hypodermis are seen to be arranged in a fairly regular, single layer over the entire surface and just inside of the cuticula. The wings in their continued growth back over the body begin to decrease in thickness and at about this time there first appear those enlarged hypodermal cells from which the vein and marginal hairs develop; these are soon followed by the other enlarged cells between the veins from which the large surface hairs are formed.

Vein hairs. Just before the appearance of these above mentioned cells the hypodermis occupiés a fairly even layer just

under the cuticula, cell boundaries are very hard to differentiate but the elongated, irregular, ovoid nuclei are fairly regular in their arrangement (Fig. 3). From the inner surface of the hypodermis come off a number of strands of protoplasm many of which, at this stage of the wing's development, pass across from surface to surface and connect the two layers of hypodermis with each other; these strands have nothing to do with the development of the wing hairs. The first indication of the trichogens, cells from which the hairs develop, is noticed in that certain of the nuclei of the hypodermis increase in size and then, with some of the surrounding protoplasm, push in from their original position towards the median part of the wing and away from the cuticula. These trichogens which first appear are situated adjacent to a vein and between it and the cuticula (Fig. 4). Nearly all of these trichogens lie along one side of the section; this is the upper surface of the wing upon which surface most of the hairs develop. The trichogen nuclei differ in position and size from the normal ones of the hypodermis, they also become more circular in outline but do not as yet differ in structure. At the same time that the trichogen nuclei wander away from the surface of the wing it is noticed that other nuclei go with them, these latter retain their normal size; they can be found in younger stages of the trichogen's growth (Figs. 5, 6, 7) and also after the hair has been developed (Fig. 8). What function these nuclei may perform is not known. This differs a little from the account of Mayer (6) who found that in Lepidoptera the trichogens first grow outward, towards the cuticula, while in Platyphylax we find that the movement is at first opposite to this and that the trichogens wander inward, away from the cuticula.

In the regular hypodermal cells each nucleus has one, sometimes two, rather small nucleoles which did not stain with hæmatoxylin or alum carmine. The trichogen nucleole, also non-staining, is at first similar to that of the other nuclei but enlarges with the growth of the nucleus until it becomes very noticeable (Fig. 6). At a later stage cell boundaries are more easily seen and the trichogens differentiate themselves from the other cells not only in this respect but also by the darker appearance of the cytoplasm; this fact, that the trichogens stain more deeply than the regular hypodermal cells was

noticed by Mayer (6). This is due to the secretary activity of these cells and shows that hair formation has already started (Fig. 7). At this stage it was difficult to find places where the young hairs could be followed for any distance because, during the wing's development, the hairs lie close against the surface and are shown in section as little circular or oval masses near the surface of the wing.

With the further growth of the trichogen its nucleus, also enlarging, begins to flatten out against the vein adjacent to which it lies; it becomes elongated and occupies a position with its longitudinal axis parallel to the surface of the wing. With the growth of the nucleus its nucleole, which has for some time been a single large one, changes and by some process, fragmentation or otherwise, becomes divided into numerous smaller pieces which are scattered irregularly around within the nucleus (Fig. 7). The flattening of the trichogen nucleus becomes especially noticeable after the decrease in thickness of the wing and it is always found to be pressed against an outer surface of the vein adjacent to which it lies. With this narrowing of the wing the nucleus not only becomes more flattened but may be bent and curved and, in studying sections, trichogens are found which contain apparently two nuclei but these are in reality sections through two parts of the same one. It might be well in this connection to mention that the vacuole, Mayer (6) or vacuoles, Schaffer (7), present in the trichogens of the Lepidoptera were not seen in Platyphylax.

After emergence of the imago sections show that the parts already enumerated are still present except the large trichogens which, as such, could not be found. The hypodermis is still present on both surfaces of the wing but the nuclei have become irregular in outline and many of them flattened against the cuticula. The functions of the trichogens ended they have undoubtedly decreased very much in size and lost their identity amongst the general hypodermal cells. (Fig. 8). This last figure does not show the final condition as the hypodermal layers become more reduced and in places almost entirely represented by the small irregular nuclei.

Large surface hairs. The special enlarged cells from which later develop the large surface hairs do not become differentiated until the trichogens of the vein and marginal hairs are plainly

visible, when they do first appear the wings have started to decrease in thickness. As already mentioned there is a stage in the development of the wing at which all cells of the hypodermis are similar and occupy an even layer just under the cuticula (Fig. 3); then some of these cells adjacent to the developing veins and at the margin of the wing increase in size and move away from the surface. With the exception of the trichogens at the two last mentioned places there is an even layer of hypodermal cells, all similar and equidistant from the cuticula, covering the areas between the veins and it is from some of these that the surface hairs develop.

Here and there in this even layer of hypodermis certain of the nuclei increase in size and move inward and away from the cuticula; these are similar to the enlarged nuclei which form the trichogens of the vein and marginal hairs except that the nuclei are different in their position on the wing and have no relation to the veins or margin. This is the first indication of the trichogens of the large surface hairs and when one (Fig. 10) is compared with the trichogen of a vein hair (Fig. 5) their similarity is apparent. Strands are seen coming from the free margin of the former and appearing very similar to part of the wall of a developing vein; they are, however, only some of the protoplasmic strands which extend from the hypodermis to the middle membrane ("Grundmembran").

As in the trichogens of the vein hairs the cytoplasm of these cells is often darker colored than that of adjacent cells and can be seen as dark streaks through the hypodermis (Fig. 11). From a surface view (Fig. 12) this same darker cytoplasm may be seen surrounding the nucleus of each trichogen but it is not noticeable in the other hypodermal cells. The same increase in surface of the nucleole that was noticed in the vein trichogens is seen, but to a less extent, in these nuclei (Fig. 13) and, when the secretion of the hair becomes active, several nucleoles are noticeable in each trichogen nucleus.

Small surface hairs. These hairs are so numerous upon both surfaces of the wing that there are very few hypodermal cells, excepting those taking part in the formation of the other kinds of hairs, from which one is not formed. In looking at the surface of a wing in which these small hairs have been developed one can examine many cells without finding one from which a small sur-

face hair has not been formed. The amount of secretion necessary for the formation of one of these hairs is comparatively small and no change is noticeable in the nuclei of the cells from which they come.

Upon the emergence of the imago these cells, as well as the trichogens of the larger hairs, decrease in size, loose their regular form and become small, irregular nuclei lying, as a rule, flat against the cuticula (Fig. 14).

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EXPLANATION OF PLATES X AND XI.

All figures drawn with a camera lucida. In all drawings the upper surface of the wing is to the left.

Cu., cuticula.
Tr. S., trichogen of surface hair.
Tr. V., trichogen of vein hair.
V., vein.

Fig. 1. Transverse section of a large vein hair. X 1700.

Fig. 2. Transverse section of one of the very long hairs found on the posterior wings. X 1700.

Fig. 3. Section through one wall of the wing from a pupa after the last larval skin has been cast and the body has started to contract. The cells of the hypodermis are as yet all similar and at no place in the section can any enlarged nuclei be found. X 1700.

Fig. 4. Section of a little older stage showing part of a vein, V, adjacent to which is an enlarged cell and nucleus, the beginning of a vein-hair trichogen, Tr. V. X 1700.

Fig. 5. A slightly older stage, after the wing has started to fold, showing three normal hypodermal cells and a vein-hair trichogen, Tr. V., near which is one of the other nuclei which move out with the trichogen. X 1700.

Fig. 6. A still older stage showing the enlarged nucleus of the vein trichogen. The greatest change over the preceding figure is in the much enlarged nucleole of the trichogen nucleus. X 1700.

Fig. 7. Section of a wing which does not as yet show the final folding. The nucleole shows the change from the single large one of the preceding stage. The cytoplasm of the trichogen is seen to be much darker than of the normal hypodermal cells and is extended out for some distance in the beginning of its development. Cuticula not drawn. X 1100.

Fig. 8. Section of a wing which has decreased very much in thickness. One vein-hair trichogen and two of surface hairs on upper surface. Middle membrane, M., m., through center of wing and connected by protoplasm to both surfaces. Cuticula not drawn. X 875.

Fig. 9. From transverse section of a wing of an imago soon after its emergence. Shows one vein hair and how the vein as well as other surface is covered by the small surface hairs. X 600.

Fig. 10. Four normal and one enlarged hypodermal cell, the latter has wandered a short distance towards the center of the wing and away from the surface; this enlarged nucleus, Tr. S., will later become that of a trichogen from which will develop one of the large surface hairs. X 1700.

Fig. 11. Two trichogens, Tr. S., of enlarged surface hairs showing the beginning of hair development. Cuticula not drawn. X 1100.

Fig. 12. Surface view of wing of about same stage as preceding. Four trichogens, Tr. S., and several normal hypodermal nuclei are shown. X 1100.

Fig. 13. Section of wing of pupa, wing folded within cuticular covering. One large and two small surface hairs. X 1700.

Fig. 14. Section showing one large and two small surface hairs. From an imago just after its emergence. X 1700.

Fig. 15. Three small surface hairs, from folded wing shortly before emergence of imago. X 1700.

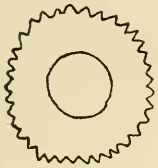


Fig.1.

Fig.2.

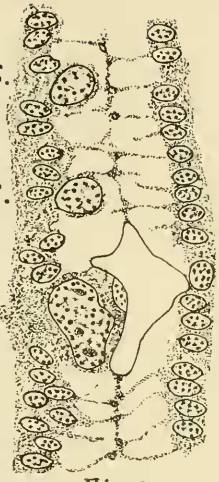
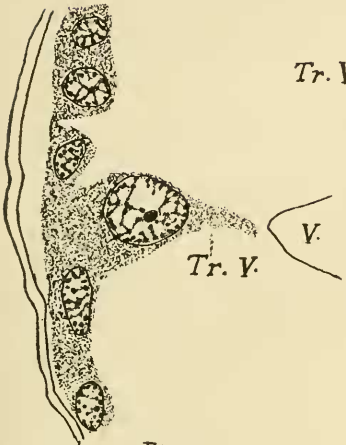
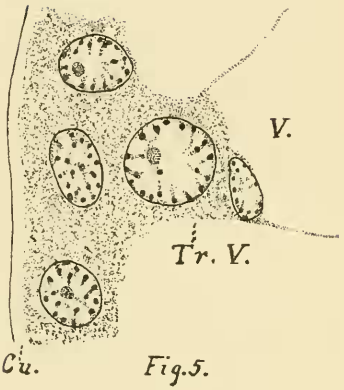


Fig.8



Cu. Fig 4.



Cu. Fig.5.

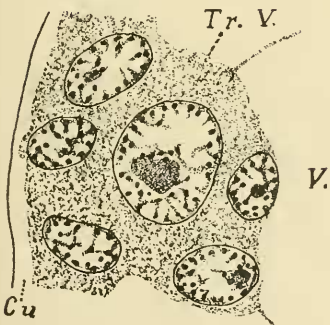


Fig.6.

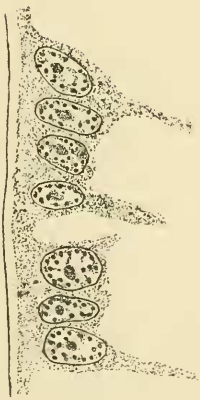


Fig.3.

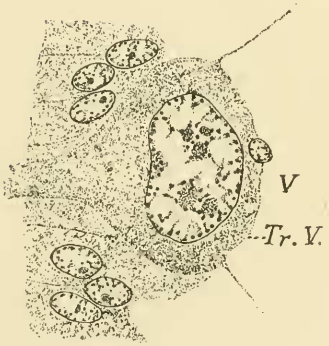


Fig.7.

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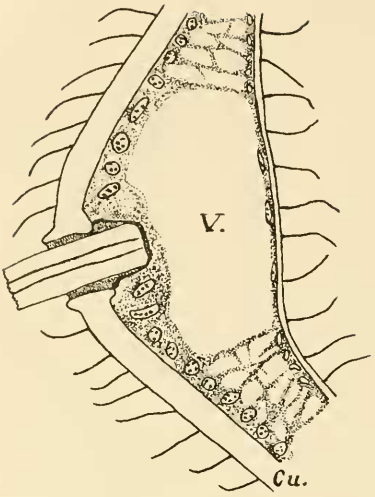

Fig. 9.

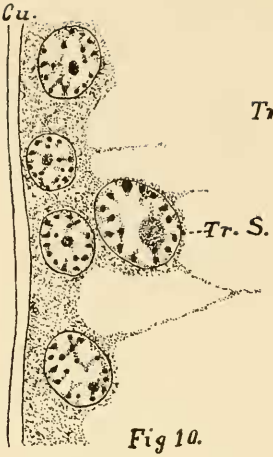

Fig 10.

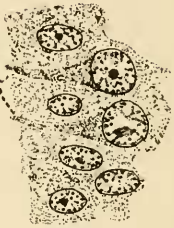

Fig. 11.

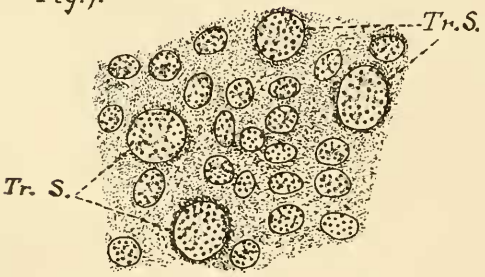

Fig. 12.

Fig. 13.

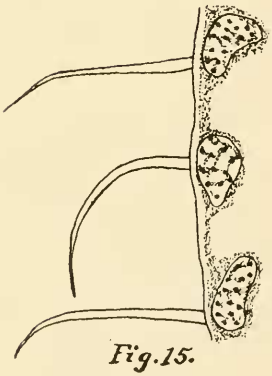

Fig. 15.

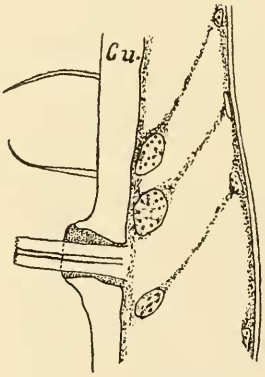

Fig 14.

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